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ORIGINAL PAPER

Insights into seasonal variation of litter decomposition and related soil degradative enzyme activities in subtropical forest in China

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Abstract: We used a litterbag method to investigate litter decomposition and related soil degradative enzyme activities across four seasons in a broad-leaved forest and a coniferous forest on Zijin Mountain in sub-tropical China. Across four seasons, we quantified litter mass losses, soil pH values, and related soil degradative enzyme activities. Litter decomposition rates differed significantly by season. Litter decomposition rates of broadleaf forest leaves were higher than for coniferous forests needles across four seasons, and maximal differences in litter decomposition rates between the two litter types were found in spring. Obvious differences in litter decomposition rates of the two litter types were found in winter, which were similar to rates in spring. Litter decomposition rates of the two litter types in autumn were significantly higher than in spring. Soil degradative enzyme activities were lowest in winter and highest in summer in most cases across four seasons.

Key words: broad-leaved forest; coniferous forest; litter decomposition; soil degradative enzyme

Introduction

Leaf litter decomposition and its resulting release of nutrients and carbon dioxide and formation of soil organic matter are fundamental processes in ecosystem nutrient cycling, carbon (C) flux, and humus formation (Hoorens et al. 2003). As a pivotal function of forest ecosystems, seasonal patterns of litter decomposition are important determinants of overall recycling of nutrients and maintenance of soil fertility in forest ecosystems (Fioretto et al. 2003). Thus, the study of the variations in litter decomposition rates across different seasons in forests is important to understanding of their functions.

Litter decomposition is driven by exoenzymes (Schimel & Weintraub 2003), and degradative enzyme activities can be used as an indicator of decomposer activities (Laiho 2006) and microbial decomposition (Moorhead & Sinsabaugh 2000; DeForest 2009). In this study, we determined the variations in degradative enzyme activities and the major degradative enzyme contributors involved in litter decomposition across different seasons in subtropical forests in a subtropical broad-leaved forest (*Quercus acutissima*) and a coniferous forest (*Pinus massoniana*) in Zijin Mountain in China.

Materials and methods

Site description

Three discrete sites, separated by approximately 50 m, were chosen in a broad-leaved forest (BF, dominated by *Quercus acutissima*) and a coniferous forest (CF, dominated by *Pinus massoniana*), located on Zijin Mountain (32°5′N, 118°48′E), Nanjing, China, with an area of 24 km^2 at an elevation of 420 m. The study areas have a subtropical humid climate. Annual mean temperature is 15.4°C, while monthly mean temperature reaches a maximum of 28.2°C in July and decreases to a minimum of 1.9°C in January. The annual precipitation is 1106.5 mm, and the rainy season is in June and July.

Experimental design

Litter mass losses were measured using the litterbag method in the field. In September 2008, *Quercus acutissima* leaves and *Pinus massoniana* needles were collected from the forest floor of the study sites (initial litter characteristics are shown in Table 1).

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All litter samples were oven-dried at 70°C for 24 h to achieve a constant weight, and then sealed into polyethylene litterbags (10 × 10 cm) with a mesh size of 2 mm. Each litterbag was filled with 5 g oven-dried litter. The bags were placed on the forest floor at the study sites seasonally, i.e., December 2008 (winter treatment, Wi), March 2009 (spring treatment, Sp), June 2009 (summer treatment, Su), and September 2009 (autumn treatment, Au), respectively. In each season, twelve sealed and labeled litterbags of each litter type were prepared and placed on the forest floor (the extra three litterbags were prepared to replace any losses), and flush with the litter layer in the forest site. There were eight treatment combinations in total: BF in winter (Wi-BF), BF in spring (Sp-BF), BF in summer (Su-BF), BF in autumn (Au-BF), CF in winter (Wi-CF), CF in spring (Sp-CF), CF in summer (Su-CF), and CF in autumn (Au-CF).

Table 1. Initial litter chemistry of *Quercus acutissima* leaves and *Pinus massoniana* needles.

Composition	Lignin ($mg \cdot g^{-1}$)	Total carbohydrate ($mg \cdot g^{-1}$)	N ($mg \cdot g^{-1}$)	Lignin : N	C:N
Leaves	301.40^{b}	485.29^{b}	9.25^{a}	32.57^{b}	52.44^{b}
Needles	385.35^{a}	526.75^{a}	7.99^{b}	48.21^{a}	65.90^{a}

Note: Data with different superscript letters in a transverse row indicate a significant difference ($p < 0.05$) using *T*-test.

Three replicate litterbags were collected seasonally approximately 90 days after placement into each study site. The soil adhering to litter samples was carefully removed, and all litter samples were then oven-dried at 70°C for 24 h to achieve a constant weight for further study. Five soil samples immediately surrounding the litterbags were also collected from each study site. All soil samples were then kept in sealed bags and immediately (after ~2 h) taken back to laboratory for further processing. Soil samples were passed through a 2-mm sieve to remove leaves, plant roots, and gravel. All replicated soil samples were then kept in a refrigerator at 4°C in preparation for further study.

Soil pH values and degradative enzyme activities

Soil pH value was measured using a glass electrode (1:2.5, soil:water ratio) after shaking the samples to equilibration for approximately 30 min (Dick et al. 2000). Monthly mean temperature and precipitation in the study site during litter decomposition were obtained from the website of the Meteorological Bureau of Jiangsu Province, China (http://www.jsmb.gov.cn).

The activities of related soil degradative enzymes involved in litter decomposition were determined spectrophotometrically with little modification: cellulase (E.C. 3.2.1.4) activity was determined using 0.5% carboxymethylcellulose solution as substrate with incubation at 50°C for 30 min (Glucose concentration was determined by colorimetric assay at 540 nm.) (Ghose 1987); invertase (E.C. 3.2.1.26) activity was determined using 10% sucrose solution as substrate with incubation at 37°C for 24 h (Glucose concentration was determined by a spectrophotometer at 508 nm.) (Ohshima et al. 2007); polyphenol oxidase (E.C. 1.10.3.1) activity was determined using 50 mM pyrocatechol solution as substrate with incubation at 30°C for 10 min (The color was determined colorimetrically at 410 nm.) (Perucci et al. 2000); catalase (E.C. 1.11.1.6) activity was determined using 8.8 mM H_2O_2 solution as substrate with incubation at room temperature for 10 min (The color was determined colorimetrically at 505 nm.) (Trasar-Cepeda et al. 1999); nitrate reductase (E.C. 1.7.99.4) activity was determined using 200 mM KNO_3 solution as substrate with incubation at room temperature for 30 min (NO_2^- concentration was determined by the spectrophotometer at a wavelength of 520 nm.) (Daniel & Curran 1981); urease (E.C. 3.5.1.5) activity was determined using 10% urea solution as substrate with incubation at 37°C for 24 h (NH_4^+-N concentration was determined by the spectrophotometer at a wavelength of 578 nm.) (Nannipieri et al. 1980); and the activity of acid phosphatase (E.C. 3.1.3.2) and alkaline phosphatase (E.C. 3.1.3.1) were determined using 0.5% di-sodium phenyl phosphate solution as substrate with incubation at 37°C for 24 h (phenol concentration was determined by the spectrophotometer at 570 nm) (Kandeler et al. 1999). Soil degradative enzyme activities were assayed within 4−5 days after sampling. The ratio of alkaline phosphatase to acid phosphatase (ALP/ACP) was calculated via their activities.

Statistical analyses

Constant potential mass loss over time was calculated by the following exponential equation (Olson 1963):

$$x_t = x_0 e^{-kt} \quad (1)$$

where x_0 is the original mass of litter, x_t is the amount of litter remaining after time t, and k is the litter decomposition coefficient ($month^{-1}$).

Data were checked for deviations from normality and homogeneity of variance before analysis. Analysis of variance was applied to assess significant differences between various treatments using DPS (version 7.05). Correlations were determined using the simple Pearson product-moment correlation coefficient. Statistically significant differences were set with p values <0.05. Three-way ANOVA was applied to test the effects of soil pH value, temperature, and precipitation on soil degradative enzyme activities using SPSS (version 17.0).

Results

Litter decomposition

After litter decomposition, cumulative mass losses of Wi-BF, Sp-BF, Su-BF, Au-BF, Wi-CF, Sp-CF, Su-CF, and Au-CF were 11.78, 13.42, 22.25, 18.37, 9.74, 10.32, 19.48, and 16.16%, respectively. Correspondingly, the litter decomposition coefficients (k values) were 0.0865 (Su-BF), 0.0735 (Su-CF), 0.0691 (Au-BF), 0.0602 (Au-CF), 0.0481 (Sp-BF), 0.0426 (Wi-BF), 0.0361 (Sp-CF), and 0.0346 (Wi-CF) (Table 2). The litter de-

composition rates of broadleaf forest leaves were 23.12, 33.24, 17.69, and 14.78% higher than those of coniferous forest needles in winter, spring, summer, and autumn, respectively (Table 2). There were no significant differences in litter decomposition rates of the two litter types between winter and spring (Table 2, p >0.05). Litter decomposition rates of the two litter types in autumn were significantly higher than those in spring (Table 2, p <0.05).

Table 2. Decomposition coefficient (k values, month^{-1}) of the two litter types across four seasons.

Season	Leaves	Needles
Winter	0.0426^{cd}	0.0346^{d}
Spring	0.0481^{c}	0.0361^{d}
Summer	0.0865^{a}	0.0735^{ab}
Autumn	0.0691^{ab}	0.0602^{b}

Note: Data with different superscript letters indicate a significant difference (p <0.05) using Tukey's Honestly Significant Differences test.

Environmental factors

Soil pH values showed slight variations by season, and pH values in BF were significantly higher than in CF (Fig. 1, p <0.05). Monthly mean temperature varied greatly by season, with a maximum of 28°C in July and a minimum of 2.2°C in January (Fig. 2). Monthly precipitation showed strong seasonal fluctuations, with a maximum of 517 mm in July and a minimum of 8.3 mm in October (Fig. 2).

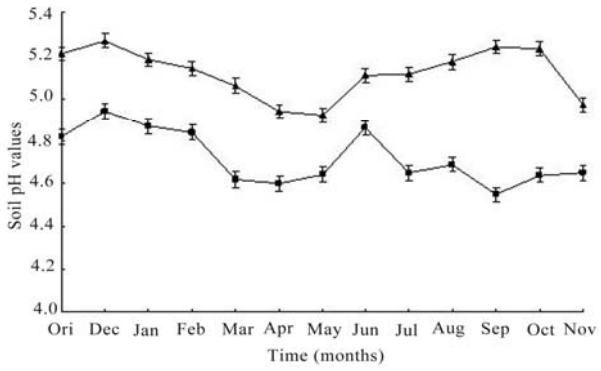

Fig. 1 Changes in soil pH values of the two forest types during litter decomposition. Symbols: filled triangle, BF; filled square, CF. Error bars indicate standard error (SE, n=3).

Soil degradative enzyme activities

Cellulase, alkaline phosphatase, and urease activities peaked in May, August, and August, respectively (Fig. 3b, f, and h), and the activities of other soil degradative enzymes (i.e., invertase, polyphenol oxidase, catalase, nitrate reductase, and acid phosphatase) peaked in July (Fig. 3a, c–e, and g). Polyphenol oxidase and acid phosphatase activities were significantly higher in CF soil than in BF soil (Fig. 3e and g, p <0.05), while the activities of other soil degradative enzymes (i.e., catalase, cellulase, urease, invertase, and nitrate reductase) were higher in BF soil than in CF soil in most cases across four seasons (Fig. 3a–d, f, and h). The ALP/ACP ratio in BF was 9.89%–79.88% higher than in CF in the corresponding treatments and incubation periods across four seasons (Fig. 4).

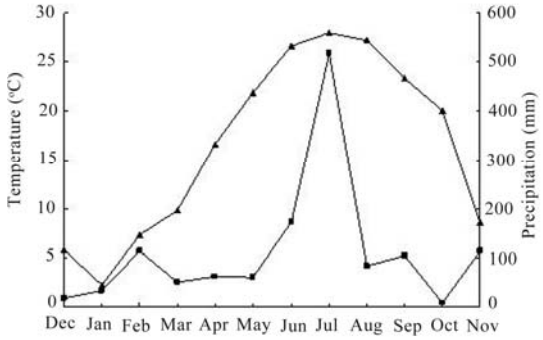

Fig. 2 Changes in monthly mean temperature and monthly precipitation in the study site during litter decomposition. Symbols: triangle, monthly mean temperature; square, monthly precipitation.

In BF soil, cellulase and nitrate reductase activities were positively correlated with litter mass losses in winter; polyphenol oxidase and urease activities were positively correlated with litter mass losses in summer; and invertase, acid phosphatase, and alkaline phosphatase activities were positively correlated with litter mass losses in autumn (Table 3, p <0.05). There were no significant relationships between soil degradative enzyme activities and litter mass losses in spring (Table 3, p >0.05). In CF soil, nitrate reductase, acid phosphatase, and polyphenol oxidase activities were positively correlated with litter mass losses in winter; invertase, alkaline phosphatase, and urease activities were positively correlated with litter mass losses in summer; and catalase, cellulase, nitrate reductase, acid phosphatase, and alkaline phosphatase activities were positively correlated with litter mass losses in autumn (Table 3, p <0.05). There were no significant relationships between soil degradative enzyme activities and litter mass losses in spring (Table 3, p >0.05).

Relationships between soil degradative enzyme activities, litter mass losses, and environmental factors

Soil pH values were significantly and negatively correlated with litter mass losses of the two forest types in winter (Table 3, p <0.05). No significant relationship was found between soil pH values and soil degradative enzyme activities in the two forest types across four seasons (Table 4, p >0.05).

Monthly mean temperature was significantly correlated with litter mass losses of the two forest types in spring (Table 3, p < 0.01), and had significant effects on the activities of most soil degradative enzymes in the two forest types across four seasons (Table 4, p < 0.05).

No significant relationship was found between monthly precipitation and mass losses of the two litter types across four seasons (Table 3, p > 0.05). Monthly precipitation had significant effects on the activities of nitrate reductase (Table 4, p < 0.05).

The interactions between soil pH values, monthly mean temperature, and monthly precipitation had significant effects on the activities of some soil degradative enzymes across four seasons (Table 4, $p < 0.05$).

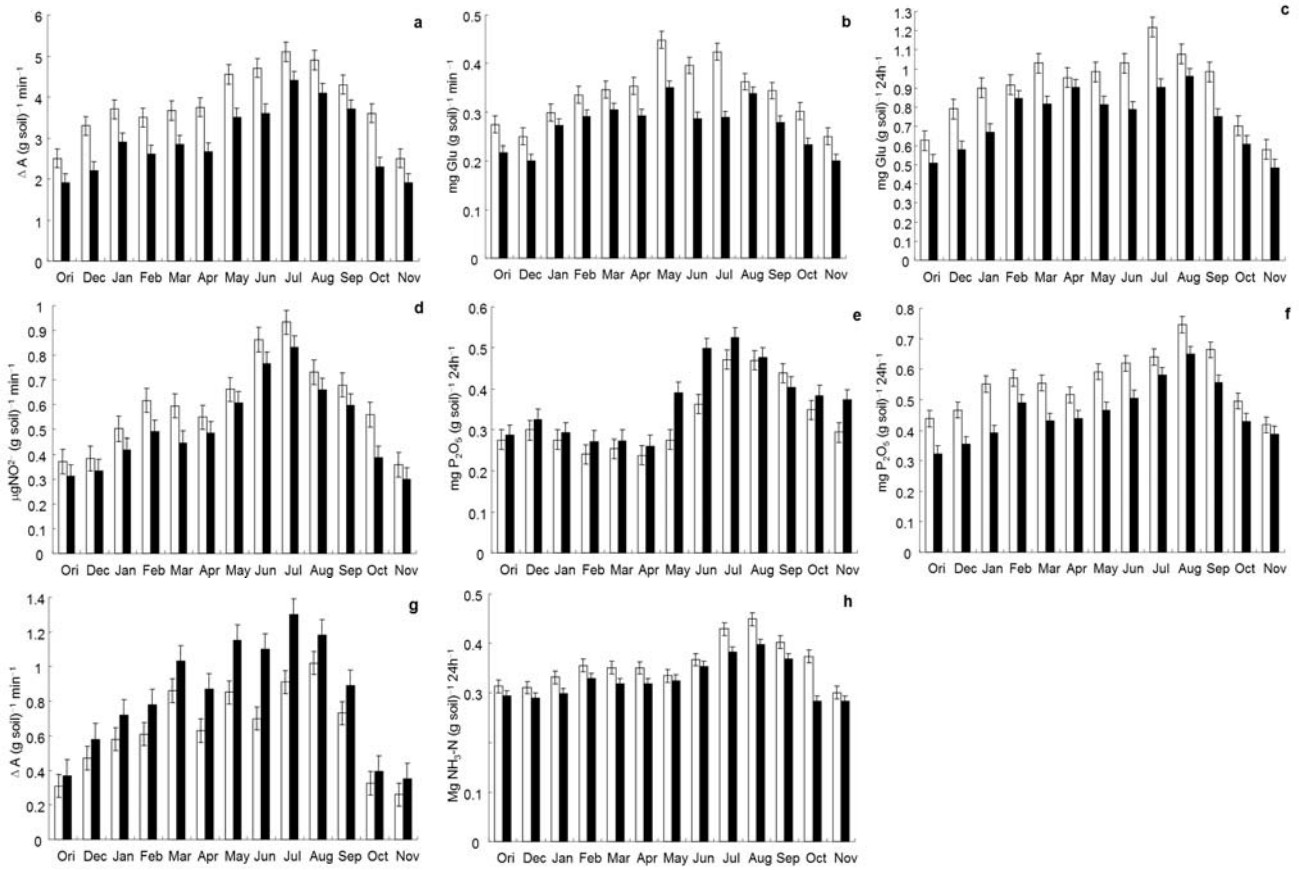

Fig. 3 Changes in soil degradative enzyme activities of the two forest types during litter decomposition. Legend: (a) catalase; (b) cellulase; (c) invertase; (d) nitrate reductase; (e) acid phosphatase; (f) alkaline phosphatase; (g) polyphenol oxidase; (h) urease. Symbols: open bar, BF; filled bar, CF. Error bars indicate standard error (SE, n=3).

Table 3. Relationship between soil pH value, temperature, precipitation, and soil degradative enzyme activities with litter mass losses of the two forest types across four seasons.

			pH	*T*	*P*	*CAT*	*CEL*	*INV*	*NR*	*ACP*	*ALP*	*PPO*	**Urease**
BF	W	r	-0.995	0.171	0.875	0.599	0.999	0.963	0.994	-0.972	0.975	0.98	0.986
		P	**0.032***	0.445	0.161	0.296	**0.011***	0.087	**0.034***	0.076	0.072	0.064	0.053
	Sp	r	-0.939	1.000	0.744	0.886	0.879	-0.625	0.553	0.545	0.459	-0.079	-0.870
		P	0.112	**0.010****	0.233	0.153	0.158	0.285	0.313	0.316	0.348	0.475	0.164
	Su	r	0.797	0.573	-0.030	0.639	-0.400	0.408	-0.505	0.934	0.858	1.000	0.993
		P	0.206	0.306	0.490	0.279	0.369	0.366	0.331	0.116	0.171	**0.003****	**0.038***
	A	r	-0.771	-0.873	-0.120	-0.947	-0.966	-1.000	-0.941	-0.998	-1.000	-0.981	-0.902
		P	0.220	0.162	0.462	0.104	0.084	**0.006****	0.110	**0.019***	**0.003****	0.062	0.142
CF	W	r	-0.995	0.166	0.872	0.667	0.979	0.954	0.996	-1.000	0.927	0.995	0.901
		P	**0.033***	0.447	0.162	0.268	0.065	0.097	**0.027***	**0.009****	0.123	**0.033***	0.143
	Sp	r	0.489	1.000	0.767	0.693	0.693	0.059	0.928	0.767	0.937	0.357	0.761
		P	0.337	**0.002****	0.222	0.256	0.256	0.481	0.121	0.222	0.114	0.384	0.225
	Su	r	-0.824	0.517	-0.098	0.695	0.831	0.995	-0.527	-0.366	0.997	0.488	0.997
		P	0.192	0.327	0.469	0.255	0.188	**0.033***	0.323	0.381	**0.024***	0.338	**0.024***
	A	r	0.978	-0.863	-0.141	-0.996	-0.992	-0.983	-1.000	-1.000	-0.998	-0.974	-0.953
		P	0.068	0.169	0.455	**0.029***	**0.041***	0.059	**0.002****	**0.005****	**0.019***	0.073	0.098

Abbreviations: A, autumn; ACP, acid phosphatase; ALP, alkaline phosphatase; CAT, catalase; CEL, cellulase; INV, invertase; NR, nitrate reductase; P, precipitation; PPO, polyphenol oxidase; Sp, spring; Su, summer; T, temperature; W, winter. * and ** indicate significant differences at the 0.05 and 0.01 probability level, respectively. *p* values equal to or lower than 0.05 are in bold face print.

Table 4. Three-way ANOVA on the effects of soil pH value (pH), temperature (T), and precipitation (P) on soil degradative enzyme activities.

P values		Catalase	Cellulase	INV	NR	ACP	ALP	PPO	Urease
BF	pH	0.837	0.222	0.939	0.958	0.163	0.541	0.748	0.330
	T	**0.001****	**0.009****	0.057	**0.002****	**0.005****	**0.014***	0.068	**0.004****
	P	0.082	0.105	0.055	**0.012***	0.064	0.272	0.232	0.103
	pH × T	**0.001****	**0.012***	0.060	**0.002****	**0.003****	**0.013***	0.073	**0.003****
	pH × P	0.079	0.106	0.053	**0.011***	0.060	0.263	0.228	0.098
	T × P	**0.027***	0.063	**0.028***	**0.004****	**0.026***	0.176	0.152	0.052
CF	pH	0.487	0.373	0.456	0.668	0.719	0.296	0.612	0.461
	T	**0.003****	0.112	0.072	**0.001*****	**0.001*****	**0.002****	**0.031***	**0.005****
	P	**0.036***	0.689	0.241	**0.010***	**0.027***	0.091	0.081	0.055
	pH × T	**0.003****	0.115	0.073	**0.001*****	**0.001*****	**0.002****	**0.029***	**0.005****
	pH × P	**0.036***	0.687	0.239	**0.010****	**0.026***	0.092	0.080	0.055
	T × P	**0.013***	0.581	0.189	**0.003****	**0.010***	0.062	**0.045***	**0.033***

Abbreviations: ACP, acid phosphatase; ALP, alkaline phosphatase; INV, invertase; NR, nitrate reductase; PPO, polyphenol oxidase. *, **, and *** indicate significant differences at the 0.05, 0.01, and 0.001 probability level, respectively. *p* values equal to or lower than 0.05 are in bold face print.

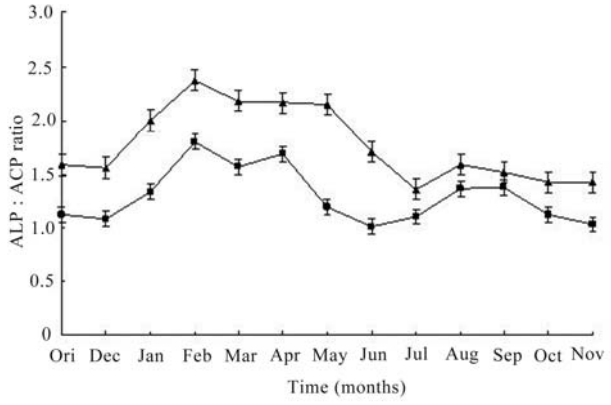

Fig.4 Changes in ALP/ACP ratio of the two forest soils during litter decomposition. Symbols: filled triangle, BF; filled square, CF. Error bars indicate standard error (SE, n=3).

Discussion

To date, numerous studies have shown decomposition rates of broadleaf forest leaves to be higher than those of coniferous forest needles in many forest ecosystems (e.g., Cornelissen 1996; Wang et al. 2010a, b). The results in this study were consistent with these studies. However, there have been no studies to clarify in which season the difference in litter decomposition rates between broadleaf forest leaves and coniferous forest needles reach the maximum. According to logical thinking, the maximum differences in litter decomposition rates between the two litter types maybe reached in summer due to high activities of soil microorganisms in summer. However, it was unexpected that the greatest significant differences in decomposition rates between the two litter types would be found in spring in this study. This may be due to the greater susceptibility in BF than in CF of soil microorganisms to increasing temperatures in spring. Some investigators concluded that ALP/ACP ratio is a sensitive indicator of microbial susceptibility to environmental changes (Dick et al. 2000). The ALP/ACP ratio of the broad-leaved forest was higher than that of the coniferous forest across four seasons and the difference in spring was higher than in the other three seasons. This suggests that the susceptibility of microbial communities to environmental changes in soils in broad-leaved forest was higher than in coniferous forest and the difference reached a maximum in spring. This is confirmed by the results of this study. The reason might be the different initial status of soil pH values, microbial composition, and/or other soil physicochemical properties between the two forest types.

Ecologists have long focused on the litter decomposition that begins in summer, the leaf-growing season, and occurs in autumn, which is the leaf-falling season (Elberling 2007). However, most studies ignored litter decomposition in winter due to the low temperature (Kirschbaum 2006; Klopatek 2008). Some studies have documented obvious litter mass losses in winter in cool temperate forests and other northern ecosystems (e.g., Hobbie & Chapin 1996; Torres et al. 2005). We also found rapid litter decomposition rates in winter. This might be due to fungi, which play an important role in litter decomposition in winter and can grow at low temperatures (Uchida et al. 2005). Another reason could be the freeze-thaw events in winter, which can enhance C and nitrogen (N) mineralization via physicochemical and/or biological effects (Yanai et al. 2004; Freppaz et al. 2007). Our results showed that decomposition rates of the two litter types in winter and spring were statistically similar but slightly lower in winter than in spring. This could be because the activities of soil microorganisms in spring and winter were similar, although the activities of soil microorganisms might be increasing in spring and relatively dormant in winter.

Although we recorded no significant differences in soil pH, monthly mean temperature, and monthly precipitation between in spring and autumn, the decomposition rates of the two litter types in autumn were significantly higher than in spring. This might be due to taxonomic differences between microbial communities in different seasons (Monson et al. 2006) and seasonal

shifts in the supply of substrate for microbial growth (Schmidt et al. 2007). Another reason might be that the freshly fallen litter above the forest floor in autumn can induce priming effects on the activities of some microbial communities (Schutter & Dick 2001).

Some studies suggested that exoenzymes can be used as an indicator of microbial decomposition (e.g., Moorhead & Sinsabaugh 2000; DeForest 2009). In this study, we found that soil degradative enzyme activities fluctuated widely by season. This might be due to variations in the supply of substrate for microbial metabolism combined with difference in temperature and/or soil moisture across different seasons. For example, the highest enzyme activities in summer may be due to the higher temperatures in summer that probably increase microbial activities (Pascoal & Cássio 2004). A second explanation might be that increased moisture from precipitation in summer accelerated the leaching of water-soluble substances from litter, and the hydrolysis without biological intervention increased nutrient availability for microbial communities in soils. Acid phosphatase activities in coniferous forest were higher than in broad-leaved forest, probably due to soil pH values in CF were nearer the optimum pH value for acid phosphatase activities (Wang et al. 2012). Polyphenol oxidase activities in CF were significantly higher than in BF, possibly because coniferous forest needles contained more polyphenols (Palm & Sanchez 1991; Kalbitz et al. 2003; Wang et al. 2012). The activities of other soil degradative enzymes in BF (i.e., catalase, cellulase, urease, invertase, and nitrate reductase) were higher than in CF, possibly because the microbial activities in BF were higher than in CF.

The type and quantity of the major degradative enzymes involved in litter decomposition in our two forest types varied across four seasons. The difference in the types and quantities of the major degradative enzymes across four seasons might have been due to differences in temperature, precipitation, physicochemical properties of the two litter types and/or litter quality in different seasons. These, in turn, might have had different effects on the activities of microbial metabolism, particularly on enzyme secretion and/or enzyme activities. Our results also revealed that C, N, and phosphorus (P) mineralization might occur simultaneously during litter decomposition across four seasons.

Litter decomposition rates in subtropical forest ecosystems reached minimum levels in winter and maximum levels in summer in this study, suggesting that temperature (perhaps also including humidity) is the major stimulating factor for litter decomposition. As a result of human activities, global climate changes are expected to continue and even become more pronounced in future (IPCC 2007). Thus, in future winter might be shortened and summer extended. As a result, the induced high rates of litter decomposition could cause an increase in levels of the greenhouse gas CO_2 into the atmosphere (Jenkinson et al. 1991). Elevated atmospheric CO_2 might also lead to a warmer climate (Trenberth 1999), which, in turn, could also induce higher rates of litter decomposition (Hobbie 1996). Thus, this could induce positive feedback to climate change in future.

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